EIGHTH REPORT.

RECENT PROGRESS IN PHYSIOLOGY.

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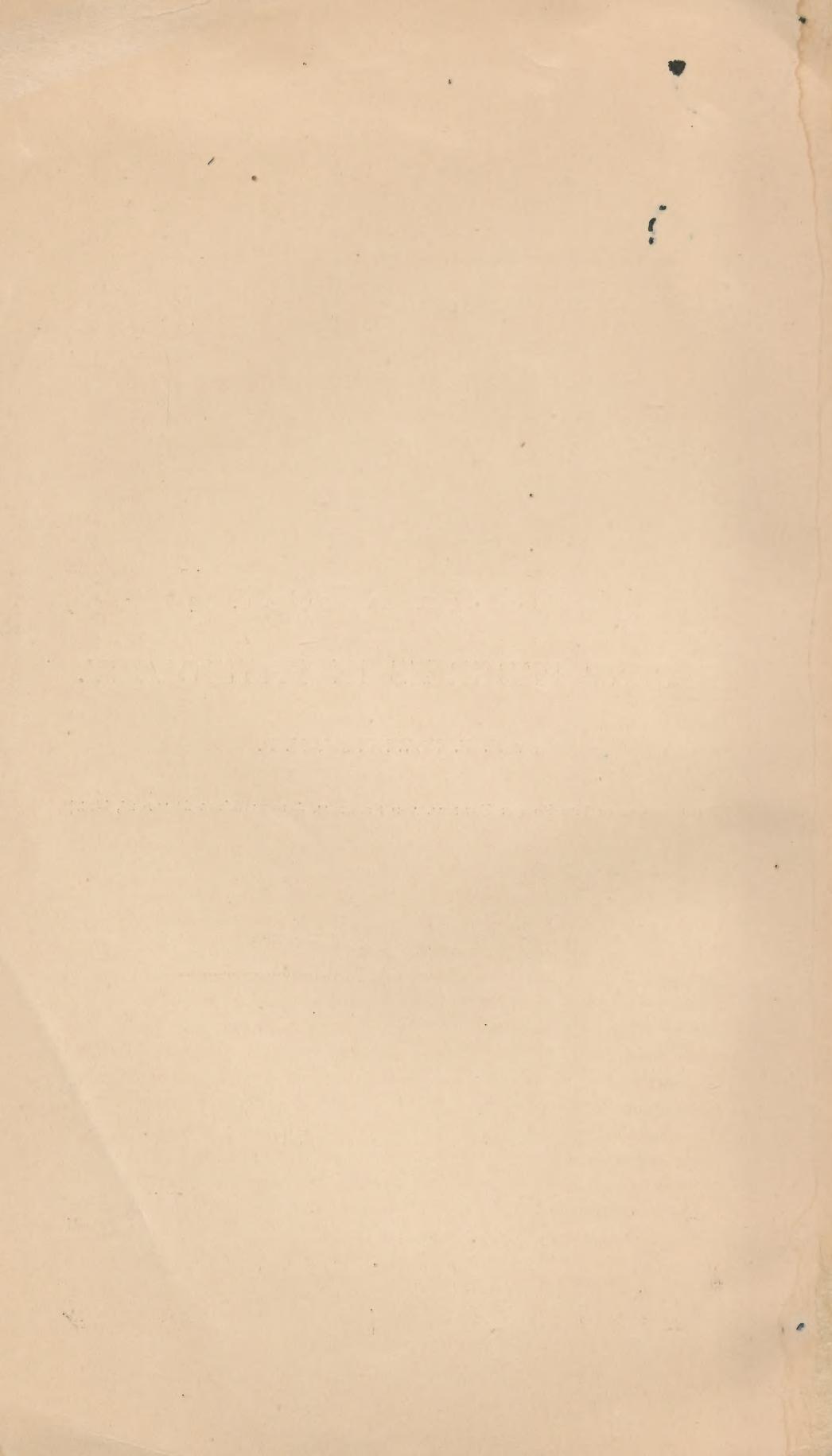
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FUNCTIONS OF THE CORTEX CEREBRI.

Investigations by Local Irritation. — In the report for July, 1873, an account was given of the then recent experiments of Hitzig, Ferrier, and others, showing that certain groups of muscles could be brought into activity by the irritation of definite points on the surface of the cerebral lobes. Since that time the subject has occupied the attention of numerous investigators, who all admit the existence of " active spots " (as Burdon-Sanderson calls them) in the cortex cerebri, but differ widely in their views of the mechanism by which the irritation of these spots gives rise to muscular movement. Three possible explanations of the phenomenon may be given : (1.) The movement is caused by the irritation, not of the part to which the electrodes are applied, but of some deeper-seated portion, in consequence of the spreading of the electric current through the cerebral substance. (2.) The " active spots " are nerve centres, *i. e.*, collections of ganglion cells, presiding over the groups of muscles which are brought into activity by their irritation. (3.) The " active spots " are not themselves nerve centres, but stand in nervous connection with the deeper-seated centres of definite groups of muscles. The movements in question are therefore of a reflex nature.

The first of these propositions has been maintained by Dupuy[1] and by Carville and Duret.[2] These authors, however, only showed that it is possible to irritate remote parts of the brain by electrodes applied on the surface, not that it is impossible to produce muscular movements by an irritation of the cortex under conditions which preclude the possibility of any but local action. That local irritation of the cortex may really produce the movements in question has been shown by Braun[3] in a series of experiments consisting in dividing with a sharp knife the connections between an " active spot " and the subjacent tissues. After this operation, which would not be likely to prevent the spreading of electrical currents to the deeper tissues of the brain, irritation of the " active spot " was found to be without effect even when the intensity of the current was made much greater than that which, before the

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[1] Examen de quelques Points de la Physiologie du Cerveau. Paris. 1873.
[2] Gazette médicale de Paris, January 10, 1874.
[3] Eckhard's Beiträge zur Anatomie und Physiologie, vii. 127.

operation, was sufficient to produce definite movements. A similar investigation made entirely independently by Dr. J. J. Putnam [1] led to the same result, except that after section of the subjacent tissues it was found necessary to increase *only slightly* the intensity of the current applied to the cortex in order to produce the same muscular movements as before. Carville and Duret deny that these experiments prove what their authors intended to show, for they maintain that the blood effused when the tissues under the "active spots" are divided is a so much better conductor of electricity than the brain substance that the currents no longer penetrate into the deeper tissues unless they are made more intense. How far this objection is valid can be determined only by careful investigations directed to this special object. It is proper to mention, however, that Carville and Duret, influenced by other considerations, have admitted in a recent work [2] that electrical irritation of the cortex " has a certain local action, and that the result of this action varies with the points of application of the electrodes."

The observations of Hermann [3] (that destruction of the "active spots" by drying or by nitric or acetic acid does not prevent the irritation from producing the usual effects, and that after mechanical removal of the "active spots" irritation of the underlying brain substance still calls forth the same movements) do not of course disprove the existence of excitable nerve tissue in the cortex, but only show that the tissue under the "active spots" is also excitable. In view of the above-mentioned positive results obtained by Braun and Putnam the negative results of Hermann's experiments are of little importance.[4]

The excitability of definite spots in the cortex being therefore regarded as well established, it remains to inquire whether the movements in question are due to a direct irritation of *centres in the gray substance* or are reflex phenomena taking place through *deeper-seated centres*, the excitable nerve tissue of the cortex (whether nerve-cells or nerve fibres) acting in this case in the same way as the terminations of peripheric nerves in an ordinary reflex action.

To appreciate the force of arguments bearing upon this point it is necessary for us to consider what information we can obtain from other sources in regard to the mechanism by which the cerebral centres are brought into connection with the motor nerves. The fact that the cervical cord contains fewer nerve fibres than the spinal nerve roots shows that the brain cannot have a direct connection with every muscular fibre, and our inability to innervate an isolated muscular fibre, or even a single muscle (except with difficulty and after much practice), is quite in accordance with this anatomical observation. Moreover, the occur-

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[1] The Journal, xci. 49.

[2] Archives de Physiologie, 1875, vii. 409.

[3] Pflüger's Archiv, x. 77.

[4] For an account of Dupuy's theory of nerves in the pia mater see the JOURNAL, xciv. 379.

rence of purposive reflex movements in animals whose cervical cord has been divided, and their apparent identity, as far as muscular mechanism is concerned, with voluntary movements, have led to the hypothesis that the cord is the seat of so-called "coördinating centres" presiding over *groups* of muscles, and that these centres may be brought into activity either by an impulse coming from without through an afferent nerve, in which case the movement is reflex, or by an impulse coming from above, for example, from a centre of volition, in which case the movement is voluntary. By an extension of the same hypothesis higher, "coördinating centres" presiding over more complicated muscular movements, for example, those of walking, have been assumed to exist in the ganglionic masses at the base of the brain.[1] It will thus be seen that, while it is very easy to decide whether a movement called forth by the irritation of a nerve trunk is direct or reflex in its character, the decision is much more difficult when the movement is the result of irritation of the cortex cerebri. For in the former case, apart from the help afforded by a knowledge of the anatomical distribution of the nerve, the character of the movement (*i. e.*, whether tetanic, purposive, etc.) and the time required for its accomplishment are usually conclusive in regard to the matter. In the latter case, however, not only does anatomy afford us little or no assistance, but, if the above-mentioned theory of nervous mechanism is correct, we cannot expect that a direct will differ materially from a reflex movement, either in character or in the time necessary for its performance. This will be evident when we consider that in both cases the impulse must be transmitted through coördinating centres which bring whole groups of muscles into action, and that it is in these centres that the delay in transmission occurs which is commonly regarded as characteristic of reflex phenomena.

The above considerations are sufficient to invalidate many of the arguments which have been brought forward to prove the reflex nature of the movements in question. Thus it has been urged by Schiff[2] that these movements are reflex because they are stopped by complete narcosis, because no tetanus is produced by a rapidly interrupted induced current, and because the time elapsing between the beginning of the irritation and the production of the movement is from seven to eleven times greater than it should be if the impulse were directly transmitted, with the normal rapidity of nerve force, from the point irritated to the muscles. On the other hand, it has been shown by Gliky[3] that the movements in question cannot, like various well-known reflex actions, be inhibited by a powerful irritation of a peripheric nerve. This writer

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[1] See Report on Pathology of Cortex Cerebri, in the Journal, xci. 111.
[2] Archiv für experimentale Pathologie, 1874, iii. 171.
[3] Eckhard's Beiträge, vii. 179.

is therefore inclined to deny to nerve centres all participation in the production of these movements, though he admits that the experiments are not decisive.

In the imperfect state of our knowledge of the conditions affecting the activity of the cerebral centres it is difficult to devise conclusive experiments, but in their absence it is interesting to notice such observations as those of Lander[1] on the brain of an idiotic boy fifteen years of age, who had had an attack of infantile spinal paralysis at three years of age and since that time had suffered from paralysis of the muscles of the trunk and neck, especially on the right side. In this brain a decided atrophy was noticed in those convolutions which, according to the observations of Betz[2] on the ganglion cells of the cortex, are to be regarded as analogous to the motor regions of the gray substance demonstrated in experiments on animals. It was noted also that the atrophy was more marked on the left side than on the right. In this connection are also to be mentioned the observations of Soltmann,[3] who found that irritation of the cortex cerebri of puppies less than nine or ten days old produced no muscular movements, and that the " active spots " on the brains of young animals differ in size and shape from those of adults. Whatever view, therefore, may be taken of the mechanism by which irritation of the cortex gives rise to muscular movements, it seems evident from these two observations that the " active spots " are regions of the cortex *whose development is connected with the power of causing contraction in certain sets of muscles.*

Not only do groups of striped muscles seem to be thus functionally connected with definite regions of the cortex cerebri, but there is also reason to believe that a similar relation exists for the heart, the bloodvessels, the spleen, the intestines, and the salivary glands. Thus it has been found by Lépine[4] that irritation, with feeble induced currents, of the post-frontal convolution of a curarized dog causes a rise of bloodtension in the crural artery of some seven centimetres of mercury. This is accompanied by an increased rapidity of the heart-beats, but if the irritation is very strong and the vagi intact, a diminution in the rate of the heart-beats results. If the irritation is applied to a spot which on an uncurarized dog would cause movements of one of the opposite feet, the temperature of this foot rises several tenths of a degree. The temperature of the foot on the same side rises also, but to a less degree, while that of the rectum remains stationary. Lépine also discovered certain spots whose irritation caused an increased secretion of saliva. Bochefontaine,[5] operating in a similar way, found four different spots on

[1] Centralblatt für die medicinischen Wissenschaften, 1875, page 225.
[2] Centralblatt für die medicinischen Wissenschaften, 1874, page 596.
[3] Centralblatt für die medicinischen Wissenschaften, 1875, page 209.
[4] Gazette médicale, 1875, No. 25.
[5] Gazette médicale, 1875, No. 52.

the surface of the brain whose irritation caused contraction of the spleen, and six spots from which movements of the intestines could be produced.

A much more decided rise of temperature in the limbs than that noticed by Lépine was observed by Eulenberg and Landois [1] as the result of the application of the actual cautery to the cortex on the opposite side. They regarded this result, however, as due to the destruction, not to the irritation of the parts in question, for they were able by electrical irritation of the same parts to obtain a slight and transient diminution of temperature in the limbs. This question will be considered in the latter part of this report.

Investigations by Local Destruction. — In all the experiments above alluded to, the motor functions of the cortex were studied by irritating the points in question and noticing what movements were produced. Another class of investigations consists in destroying the part of the cortex whose function is to be studied, and observing what muscles become incapable of voluntary movement. In experiments of this sort it was soon found that, whatever may be the immediate result of the mutilation, the paralysis wholly or in great part disappears if the animal survives the operation a few days or at most one or two weeks. To explain this a sort of vicarious function of the different portions of the cortex has been assumed, but various opinions have been held as to the parts which are thus capable of assuming each other's functions. Carville and Duret [2] consider that every part of the cortex of each cerebral lobe may act for every other part of the cortex of the *same* lobe, but deny that the functions of any portion of one lobe can be assumed by the corresponding (or by any other) part of the *opposite* lobe. This opinion derives apparent support from the fact that after the disturbances produced by a local destruction of cortical substance on one side have passed away, they may be reproduced by a further destruction on the same side, but not by a destruction of the corresponding part of the opposite side.

Soltmann,[3] on the other hand, is of the opinion that when a portion of the cortex is destroyed, its functions may be performed by the symmetrically situated portion on the opposite side. He supports this view by the following experiment. On a dog four or five days old the cortex of the whole præ-frontal and of part of the post-frontal lobe on the left side was removed. The animal showed no motor disturbances, and recovered completely from the operation, being distinguished only by a somewhat smaller size from the other pups of the same litter. Three months later the brain was exposed on the right side and the centre for the fore leg irritated. Movements of the leg not only of the

[1] Centralblatt für die medicinischen Wissenschaften, 1876, page 260.
[2] Archives de Physiologie, 1875, page 453.
[3] Jahrbuch für Kinderheilkunde, ix. 106.

opposite but also of the same side followed this irritation. It was found impossible by any variations of the intensity of the electric current or of the point of application to produce movements in the leg of the opposite side alone. When, however, the centre for the hind leg was irritated, movements were produced in the leg on the opposite side alone, the corresponding centre on the other side being apparently still intact.[1]

The fact that such diametrically opposite opinions can be held by intelligent observers shows clearly the need of renewed investigations and improved methods. Goltz has accordingly in a recent article [2] given the results of a series of experiments made in a way which seems calculated to avoid some of the difficulties experienced by other observers. One of the principal obstacles in the way of arriving at a correct solution of this question is the difficulty of keeping animals alive after the loss of a considerable portion of the cortex cerebri. Profuse hæmorrhage or inflammation of the brain substance often leads to a fatal result before the most important observations can be begun. To avoid these difficulties, Goltz had recourse to a method of removing the cerebral substance which is often employed for making anatomical preparations of the cerebral blood-vessels, namely, washing it away by a jet of water thrown with force sufficient to break up the delicate brain tissue without greatly injuring the firmer blood-vessels. The jets of water were applied by means of canulæ variously formed and inserted through openings trephined in the skull. For a very circumscribed destruction of the cortex a single opening was sufficient. For a more extended operation several holes were made near each other, and the brain substance between them removed by a process of tunneling. By a series of operations of this sort, which, however, were by no means bloodless, Goltz succeeded, in one instance, in washing away all the convolutions of one of the cerebral lobes which could be reached by openings through the skull. The animal lived in this condition for several weeks, and was used for numerous observations.

As the result of his investigations, Goltz maintains that the extent, and not the locality, of the injury is of importance in determining the nature of the disturbance produced ; *e. g.*, the effect of the operation is the same whether the brain substance is washed away in the anterior portion of the so-called " excitable zone " of Hitzig or far back in the posterior lobe. This want of agreement with the results obtained by other observers may perhaps be partly explained by the fact that in all Goltz's operations a comparatively large portion of the brain was destroyed ; *e. g.*, where the jet of water was applied through a single open-

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[1] See also Brown-Séquard's observations on vaso-motor and other disturbances on the *same* side as the cerebral lesion, Archives de Physiologie, 1875, page 854.

[2] Pfluger's Archiv, xiii. 1.

ing in the skull, the diameter of the excavation thus produced was about 1.7 centimetres.

The author describes the results of unilateral destruction of the cortex cerebri as disturbances (1) of sensation, (2) of vision, (3) of motion, all on the opposite side.

I. *Sensation.* Immediately after an extensive destruction of the cortex the animal is often completely anæsthetic on the opposite side. Pinching and pricking of the limbs and face call forth no expression of pain. This condition is, however, transient. A few days after the operation painful impressions are felt all over the body, but less distinctly on the opposite side, as may be shown by observing the weights which are sufficient to produce annoyance when placed on the different paws. To this condition of impaired sensibility, which is found to be very persistent, the author attributes, in part at least, various awkward movements of the limbs on the side opposite to the injury. Thus a dog with an injury to the cortex on the left side, when placed upon a table, is apt to fall off whenever, in moving about, his right feet come near the edge, because, according to Goltz, his sensibility is so far impaired on that side that he does not perceive quickly enough that he is treading on nothing. Disturbances of vision and motion doubtless also contribute to this result.

II. *Vision.* Blindness on the opposite side results from an extensive destruction of the cerebral cortex. This is at first so complete that the animal in moving about strikes its head against obstacles on that side. Afterwards sight is so far recovered that obstacles are avoided, but there is a persistent defect of vision, in consequence of which objects seen with that eye fail to call forth their usual emotions. Thus a dog with an extensive destruction of the cortex on the left side, and with the left eye extirpated, learns to move about without running against obstacles, but shows no fear of objects which before the operation had excited great terror, does not recognize a piece of meat held before his face, and is not frightened when held outside of a window, as is the case with an unmutilated dog. To explain these phenomena, Goltz makes the hypothesis that a dog thus operated on has very imperfect sensations of the position and color of objects whose images are thrown upon his retina; that everything appears gray and indistinct, as if surrounded by a mist. He therefore sees objects sufficiently well to avoid them in moving about, but gets very imperfect ideas of their nature. Another hypothesis, which seems quite as reasonable, would be that the retinal images produce their normal sensations, but that the power, acquired by experience, of interpreting these sensations has been lost in consequence of the injury.

III. *Motion.* Extensive destruction of the cerebral cortex causes at first a paralysis on the opposite side, so complete that the animal in at-

tempting to stand falls upon that side. After a few days, control over the limbs is so far restored that the animal moves about in an apparently perfectly normal manner. A close examination, however, reveals a variety of motor disturbances which are very persistent in their character. In the first place, if the animal is moving on a very smooth floor the feet on the side opposite to the injury often slide out from under it. Even when lying quietly the animal often allows its legs on that side to assume, or be brought into, very awkward positions, without exhibiting any annoyance. These phenomena may depend to a great extent on the diminution of sensibility above described, but there are other motor disturbances which cannot be thus explained. For instance, a dog with an injury to the cortex on the left side does not use the right fore paw to reach and hold its food, nor to scratch away the earth for the purpose of burying a bone. If trained to give the fore paw at command, a dog thus operated on gives invariably the left paw, and if by long persuasion and reiterated commands the animal is finally taught to give the right paw, a further destruction of the cortex on the same side as before produces the former helpless condition. In other words, it is the power to use the paw, not as a locomotive organ, but *as a hand*, which is affected by the injury.

It will thus be seen that the effects of destruction of the cortex are of two sorts, namely, transient and persistent. It is the latter only which, according to Goltz, are to be regarded as indicating the functions of the part destroyed, and which he calls therefore " phenomena of deficiency " (*Ausfallerscheinungen*). They may perhaps be best described collectively as a failure on the part of the animal to make an intelligent use of its sensations, and its power of motion. The former, *i. e.*, the complete loss of motion, sensation, and vision, he regards as due to an inhibitory process, starting from the wound in the brain and acting upon deeper-seated centres. The phenomenon is therefore similar to the temporary absence of all reflex movements in an animal whose cervical cord has been divided. If this theory is correct, it is necessary to suppose that the mechanical irritation due to the removal of a portion of the cortex acts not only in a very different way, but over a very different extent of brain substance from an electrical irritation applied to the same spot. From this point of view Goltz regards the immediate results of local destruction of the cortex as observed by Hitzig [1] as inhibitory phenomena, and dissents from Hitzig's conclusion that the disappearance of the disturbances produced by the injury indicates that some other portion of the cortex has assumed the function of the part destroyed. As conclusive against Hitzig's view he instances his own experiment in which a dog with the *whole surface* of a cerebral lobe washed away moved his limbs, head, tongue, eyes, eyelids, ears, jaws, and tail in a perfectly normal way.

[1] Reichert and Du Bois Reymond's Archiv, 1874, page 392.

Eulenberg and Landois, whose observations were alluded to in the first part of this report, found that cauterization of Hitzig's centres for the movements of the limbs caused a rise of temperature in those parts amounting to from 5° to 7° C., and lasting two or three days. Their statements have recently been confirmed by Hitzig.[1] It is difficult to reconcile these observations with those of Lépine (on the rise of temperature in the limbs caused by irritating the cortex), except on the supposition that the phenomenon depends upon the irritation and not upon the destruction of the parts, as the authors suppose. This view is not inconsistent with the authors' observation[2] that feeble electrical irritation of the cortex caused a diminution of temperature in the limbs ; for in the first place this cooling was very slight in amount (0.2° to 0.6° C.) and was not a very constant phenomenon, and in the second place there is reason to believe that irritation of the cortex by the actual cautery has a very different effect from that produced by electricity.[3] By an extension of Goltz's theory it might fairly be assumed that destruction of a portion of the cortex causes a temporary inhibition of vaso-motor centres as well as of those of locomotion, vision, etc. This view is quite in accordance with Brown-Séquard's[4] recent observation that all the effects of section of the cervical sympathetic may be produced by cauterization or " thermic irritation " of the cortex. In this case, however, the results were produced on the *same* side as the operation.

[1] Centralblatt für die medicinischen Wissenschaften, 1876, page 323.
[2] Centralblatt für die medicinischen Wissenschaften, 1876, page 262.
[3] See Brown-Séquard, loco citato.
[4] Loco citato, page 864.